THE WESTERN AUSTRALIAN CHRISTMAS TREE.

NUYTSIA FLORIBUNDA (THE CHRISTMAS TREE)—ITS STRUCTURE AND PARASITISM.

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(*Read 8th April*, 1919.)

Nuytsia floribunda, the Christmas Tree, is perhaps the most interesting member of the flora of Western Australia. It is confined to the South-Western division of the State, being found from the Murchison River round to Esperance. The tree finally reaches the height of 30-35 feet, and frequently two or more trunks arise together. At Christmas time the tree is a brilliant blaze of orange flowers, which are borne on dense racemes at the ends of the branches. The immense development of flowers is all the more remarkable since so few fertile seeds develop. Many trees do not develop a single seed; others may develop a number—a very small number in comparison with the tremendous number of flowers—but very few of these are fertile. Whether fertile seeds will produce mature plants is a question which will be discussed later in this paper.

The failure of the tree to produce much seed may be the direct result of the large production of blossom. A great deal of stored food material is used up in the flowering period and in Nuytsia where blossom is so abundant the resources are too much depleted to provide enough food material for the maturing of the fruits. This is borne out by the condition of the mucilage in the plant before and after flowering. Before flowering the mucilage canals are full of a milky fluid in such quantity that quite a large amount is exuded when a root or branch is broken or cut. This rapidly coagulates and blackens on exposure to air. It is very palatable to some animals, especially pigs, which root up the roots for yards if they are close to the surface. During the flowering period it decreases rapidly in amount and loses its milkiness, until at the period when the tree should be fruiting the exudation from a broken root or branch is almost nil.

That this non-production of fruit is probably due to the large amount of blossom formed is also borne out by the fact that the same phenomenon occurs in the case of cultivated trees, such as the apple and the pear. Very frequently such trees have a tremendous development of blossom which results in hardly a single fruit. Thinning out of the blossoms results in the production of a good yield of fruits for two reasons—firstly there are fewer fruits to be supplied with food material, and secondly a great deal of energy has been saved by the loss of the thinned-out blossoms.

STRUCTURE.

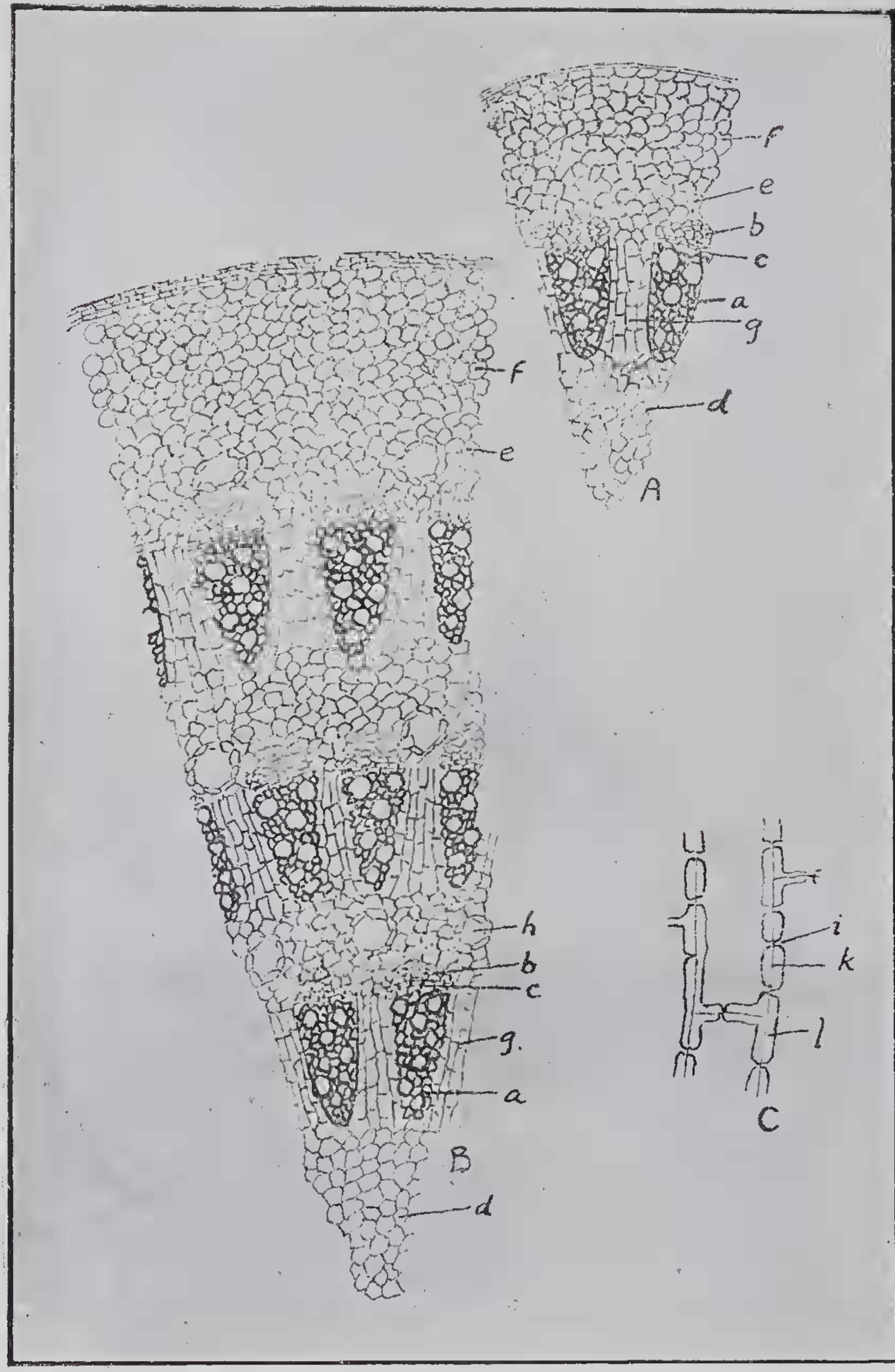
On digging down it is found that long underground stems run out from the Christmas Tree, sometimes for great distances (one at Como was traced for 120 yards), and giving off aerial branches having the appearance of trees at intervals along their length. Small plants, which might be taken for seedlings, are frequently found in belts of country where the Christmas Tree is common and almost invariably these are found to be suckers from this long stem. The production of suckers explains why Nuytsia is so common throughout the South-West in spite of its extremely small production of fertile seeds.

The growth of the stem is peculiar both microscopically and macroscopically, the second peculiarity following from the first. A very noticeable character is the extreme brittleness of the branches and roots, quite thick members snapping under quite a small pressure. This is not the case with the young twigs of one year's growth. It only takes place after secondary growth, and the explanation lies in the unusual and remarkable method of secondary growth of the tree. This is similar in both stem and root, when allowance has been made for their difference in primary structure.

In transverse section the young stem is quite normal. (Fig. 1. (A).)

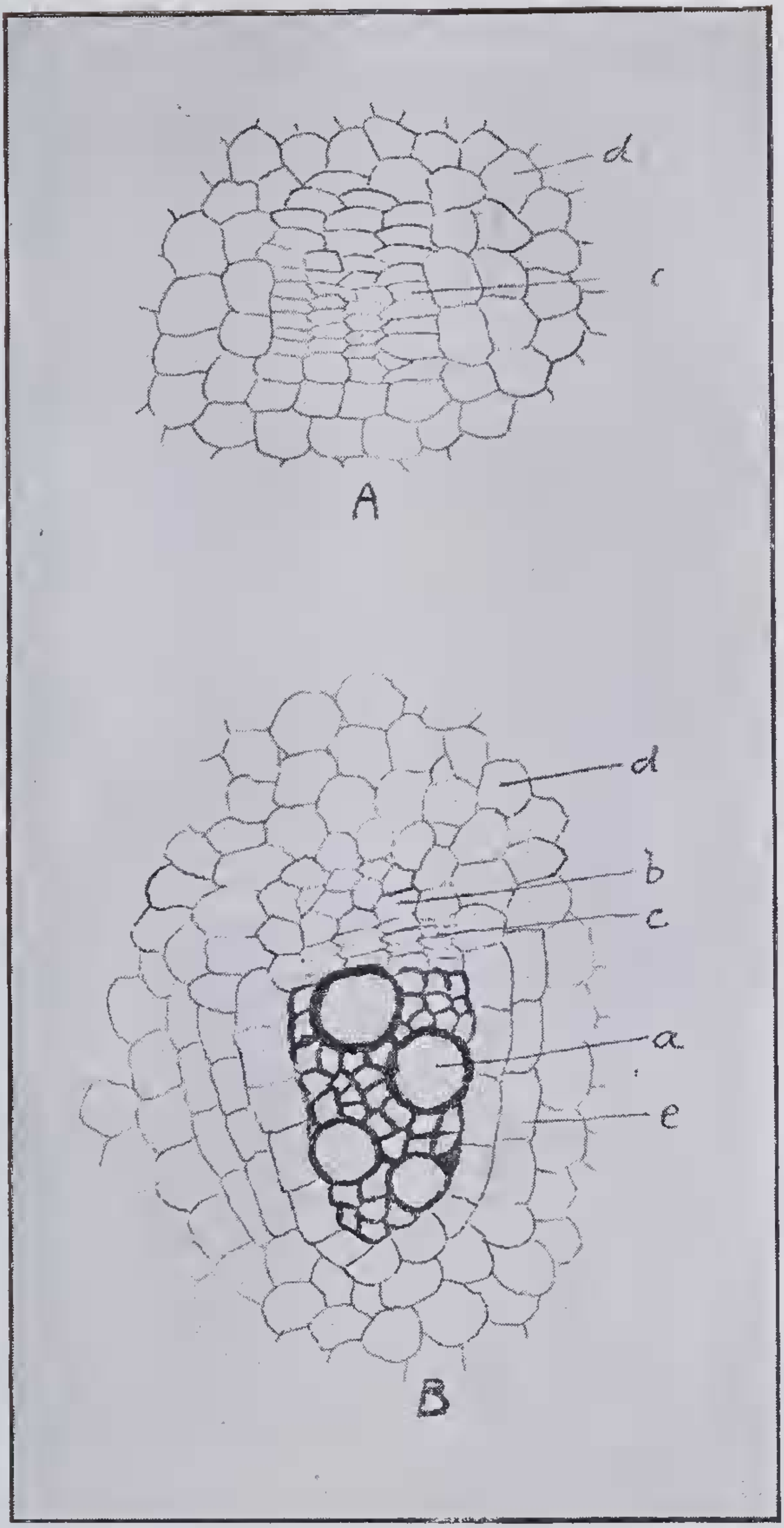
The central zone of pith is surrounded by the vascular bundles and these again by the cortex. In the normal dicotyledonous stem the cambium between the xylem and phloem elements divides forming xylem elements on the inner side and phloem elements on the outer side. In this way a cylinder of wood surrounded by phloem and cortex is produced. In the Christmas Tree the mode of growth is at first normal. There is a meristematic layer between wood and phloem of the primary bundles and this divides until they have reached a certain size, when it loses its function and a new cambium is formed in the thin-walled cells of the inner cortex. This cambium is not continuous round the stem but occurs in patches several cells in width. The cortex is divided into two fairly definite layers, the cells of the inner layer being thinner-walled and its cells smaller and more compact than those of the outer. When the new cambium is formed, several of these cells start to divide at different points round the stem forming typical cambium cells.

Fig. 1.



A. Young stem.
B. Old stem showing three rings of bundles.
C. Medullary Ray.
a, xylem; b, phloem; c, cambium; d, pith; e, inner cortex; f, outer cortex; g, interrupted medullary ray; h, mucilage canal; i, pore;

Fig. 2

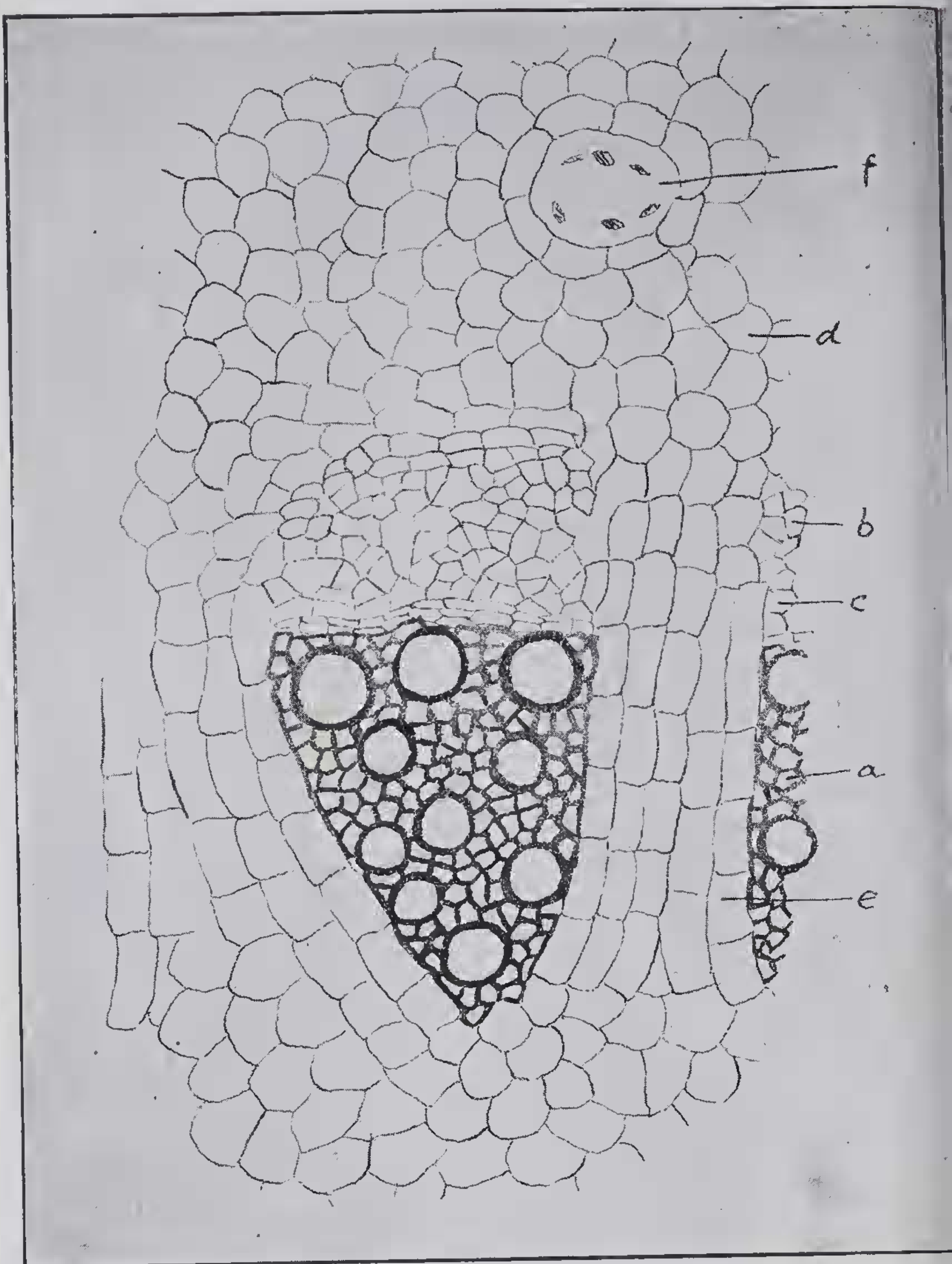


A. Cambium formed from thin walled cells of inner cortex.

B. Later stage in development of the bundle. Xylem and phloem elements have been formed from the cambium.

a, xylem; b, phloem; c, cambium; d, inner cortex; e, medullary ray.

Fig. 3.



Bundle, medullary rays and mucilage canal.
a, xylem; b, c, phloem; d, cells of inner cortex; e, medullary ray; f, mucilage canal showing proteid bodies in the mucilage.

By repeated division phloem cells are cut off from these dividing cells on the outer side and xylem on the inner side (Fig. 2B). This cambium continues to grow to a certain stage when it, too, loses its power of further division and another set of new cambiums is formed out in the inner cortex in a similar manner to that described above. This is repeated continually so that successive rings of vascular bundles separated by thin-walled cortical tissue are produced (Fig. 1B).

Short medullary rays run between the collateral bundles but these are only the length of the xylem and rarely any longer. They do not run through the cortical tissue and connect with the medullary rays of the next ring. The walls of the medullary rays are pitted (Fig. 1C). Pits are often found in the walls of the cortical and the pith cells as well as in the medullary rays. Viscum, another member of the family, also has cortical cells with pitted walls through which there is protoplasmic connection between adjacent cells.

Mucilage canals traverse stems, roots, and leaves. They are formed by breaking down of long rows of cells. In the young stem there is one canal in the pith. As the stem grows older more of these appear in the pith and in the inner cortex. When new layers of cambium are formed in the cortex these are always outside the mucilage canals so that canals are found in the cortical tissue between the successive rows of bundles. A canal less definite in structure runs along the posterior side of the bundle of the leaf.

This peculiarity in the internal structure of the stem is also responsible for the strange macroscopic appearance of the Christmas Tree

The young branch is at first upright, but as it increases in thickness it takes on a downward curve until the angle becomes too steep, when it ceases growth and another branch further back takes its place and continues the growth until it, too, becomes too steeply curved, when another branch takes its place. The portion of the branch below the end and the new main branch generally dies back. This strange mode of growth is responsible for the characteristic rugged appearance of Nuytsia. No such curvature is found before secondary growth has taken place and curvature is not due to a more rapid growth on the upper side of the stem. Branches of three or four years' growth because of their peculiar internal structure are very easily bent under comparatively light pressure, and the weight of the leaves and blossoms (that of the latter being very considerable) causes the gradual downward curvature.

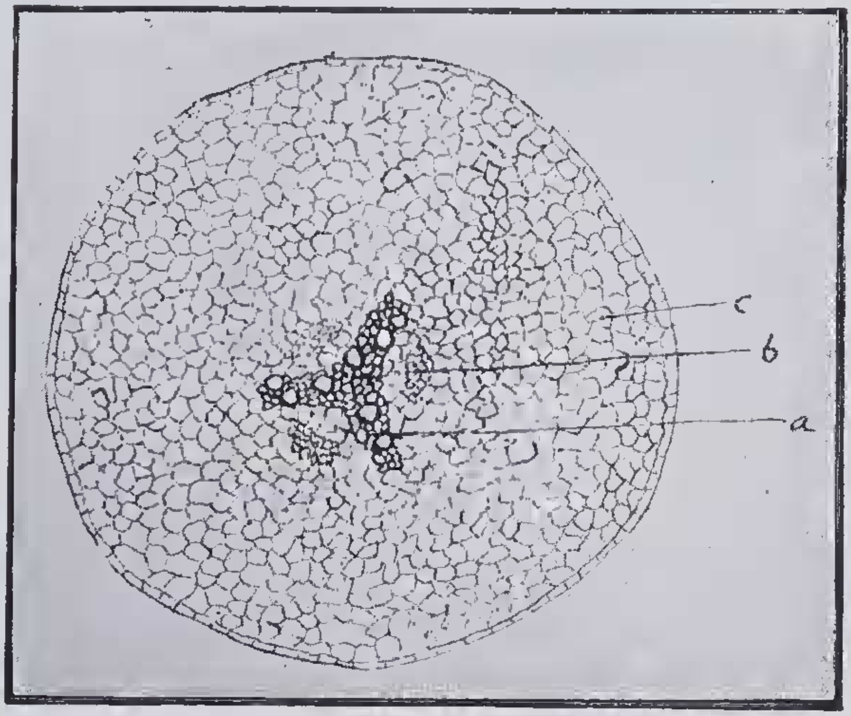
The secondary growth of the root is of essentially the same character as that of the stem, though differing a little because of the normal structural difference of stem and root. Like the young stem, the young root is normal in structure (Fig. 5) and may be diarch or triarch.

Fig. 4.

Christmas Tree, showing downward bending in the branches.

Here again the cambium between wood and phloem divides to a certain extent forming secondary elements, but soon loses its function, and new patches of cambium are developed out in the inner cortex. The xylem of the elements formed from these second cambiums connects with the central xylem strands (which consist

Fig. 5.



Young root of Christmas Tree.
a, xylem; b, phloem; c, cortex.

of the primary and a certain amount of secondary wood) so that the protoxylems are surrounded by later formed wood elements (Fig. 6).

When this second ring of cambium patches has divided to a certain extent it ceases to divide and another new cambium is formed outside in the inner cortex. The bundles formed from this are not connected with the previous year's bundles, but are separated, as in the stem, by a layer of cortical tissue. All further growth in thickness after this is similar to that in the stem. The result of this method of growth is that the old root shares the stem's characteristic of brittleness. Mucilage canals and interrupted medullary rays occur here as in the stem.

PARASITISM.

Nuytsia floribunda is the sole representative of its genus. It is classified systematically with the Loranthaceae,* and on account of this its autonomy has long been questioned, though no definite evidence was brought forward.

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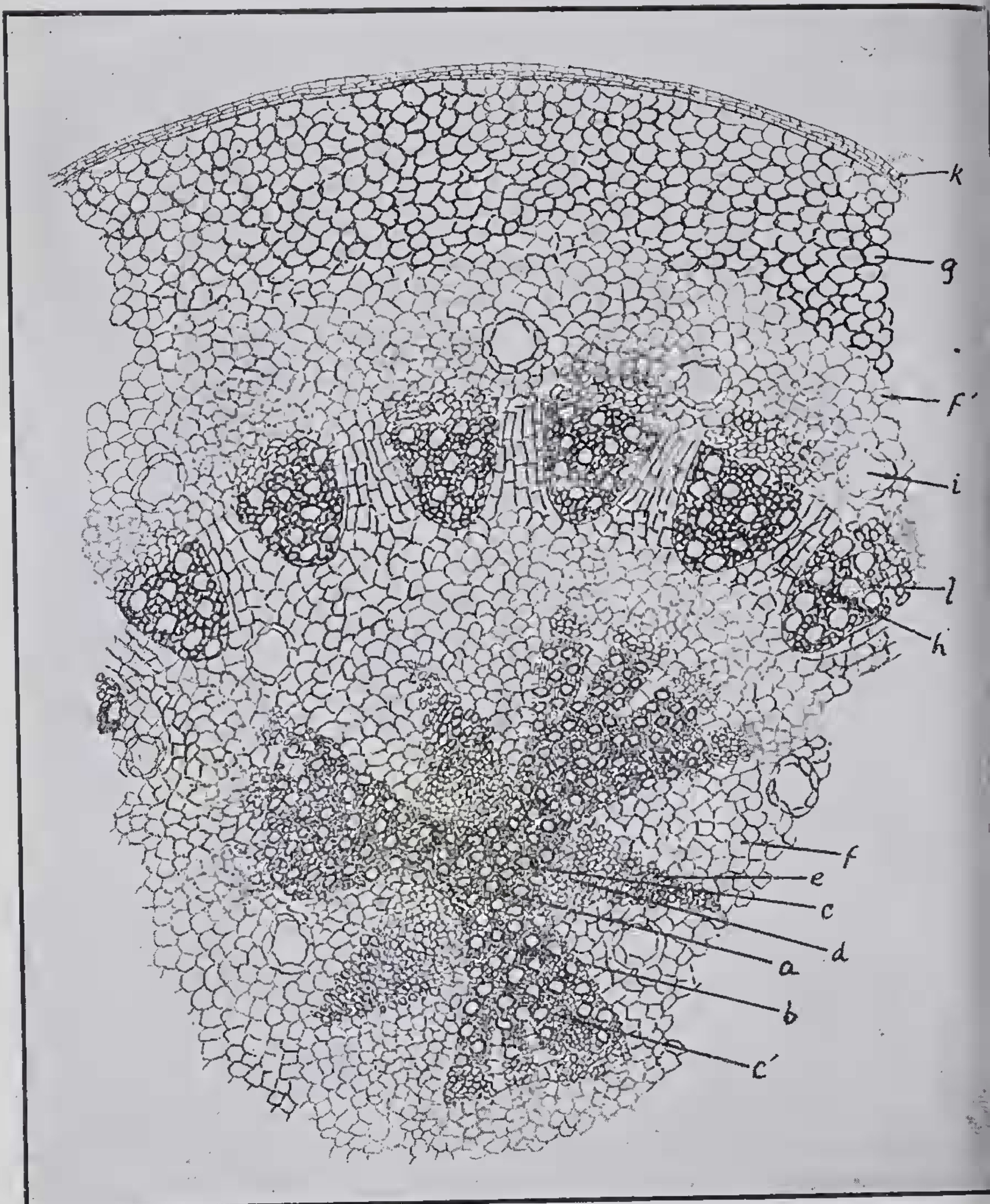
* See end of paper, p. 88.

Fig. 6.



Old root of Christmas Tree.

a, position of primary xylem (see Fig. 5); b, protoxylem; c, secondary wood added to primary xylems by a certain amount of division of the cambium; c′, secondary xylem formed from cambium formed from inner cortex; d, phloem; e, sclerenchymatous strand external to primary phloems; f, f′, inner cortex; g, outer cortex; h, medullary ray; i, mucilage canal; k, cork; l, bundles formed by the second cambiums formed in the outer cortex.

The tree is frequently in places where parasitism would seem unlikely. Dr. Diels, on finding it growing on barren and healthy sand-scrub, the solitary tree for miles round, considered it a far-fetched assumption that the tree would draw on the dwarf bushes at its base for nourishment, and concluded "Till some counter evidence is produced we must adhere to the autonomy of Nuytsia floribunda."

Mr. W. Webb, of King George's Sound, furnished some notes on Nuytsia floribunda in response to some questions asked by Baron von Mueller and these were published in the *Victorian Field Naturalist* in 1894. They are brief and may be given in full:—

> We can find thousands of what at first sight appear to be seedlings but on tracing the roots we always find them growing from the roots† of parent trees, and therefore we think these supposed seedlings are nothing more or less than suckers. Up to the present we have not been able to find the roots attached to anything; they shoot in all directions and for great distances but never penetrate the soil deeply, but are always found some few inches below the surface. In this manner they may and probably do receive their sustenace from decaying vegetable matter, such as the roots of numerous species of shrubs amongst which Nuytsia usually grows. As this plant has a pretty wide range in West Australia, would it be worth while to ascertain what trees and shrubs occur in every locality where Nuytsia is found? So far as my memory serves me, I feel certain that a great difference will be found in the species of plant life at different places. My own opinion is that Nuytsia is an independent tree and it requires certain conditions in the soil which can only be given to it by certain other species of plants. However, I have nothing to advance in proof of the above except that I have never found the roots attached to the roots of any other plants.

Harvey (Hooker's Journal of Botany VI., 219) thought it highly probable that there was connection between the roots but could offer no proof. Dr. Morrison apparently made some investigations according to a reference by Diels, but I have been unable to find a record of his work. In the Western Australian Year Book, 1902-1904, however, he refers to Nuytsia floribunda as "a non-parasitic tree of the Mistletoe family." It would appear, therefore, that authorities up to the present, while suspecting the parasitic nature of the plant, have had to admit the absence of definite proof, and in some cases they have finally concluded that the Christmas Tree is independent.

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† The roots referred to are really stems. D.A.H.

Figs. 7 and 9.

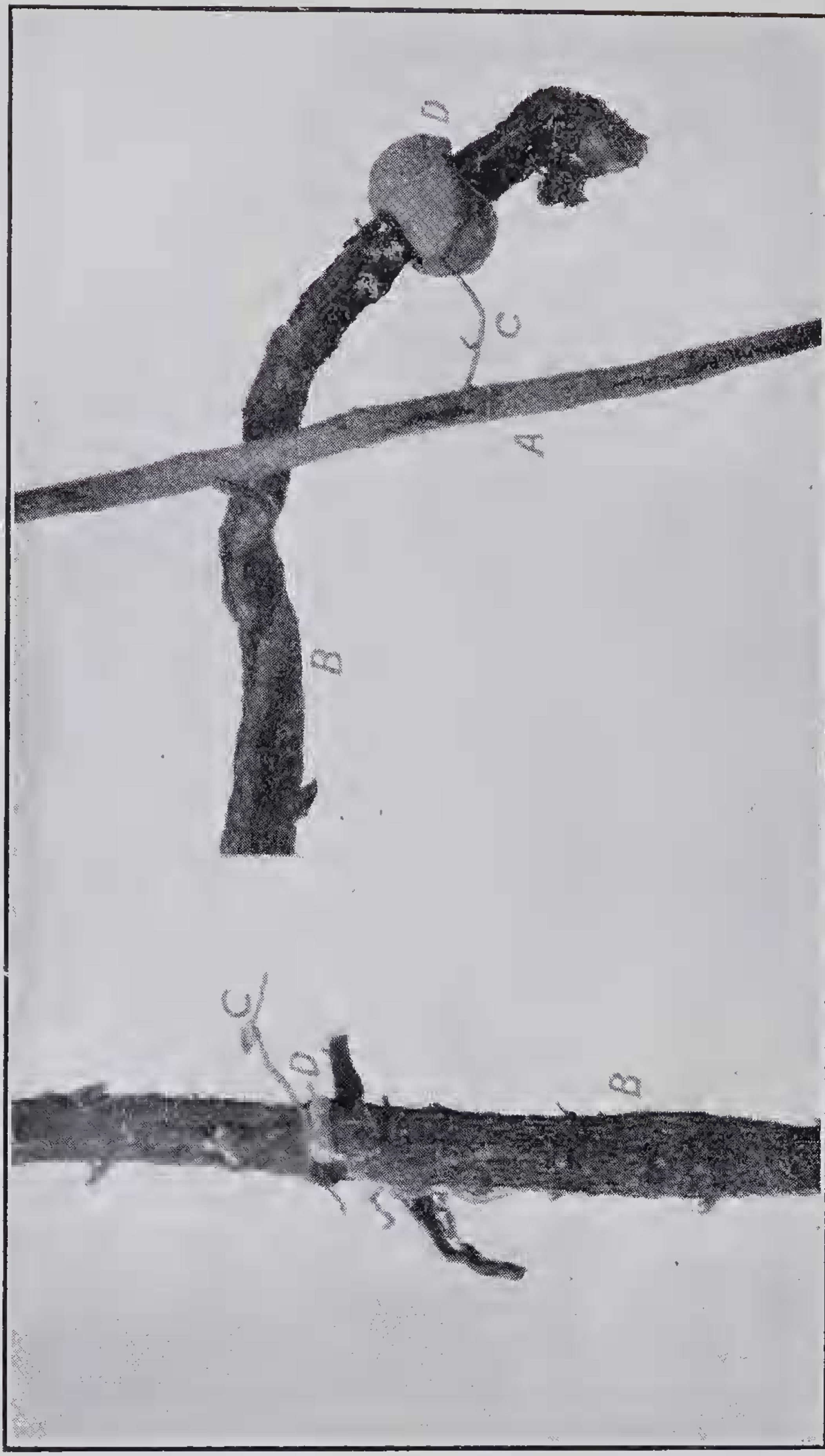


Figure 7.—Commencement of attack on Christmas Tree root on root of Jacksonia furcellata, showing the two fleshy arms commencing to surround the root.

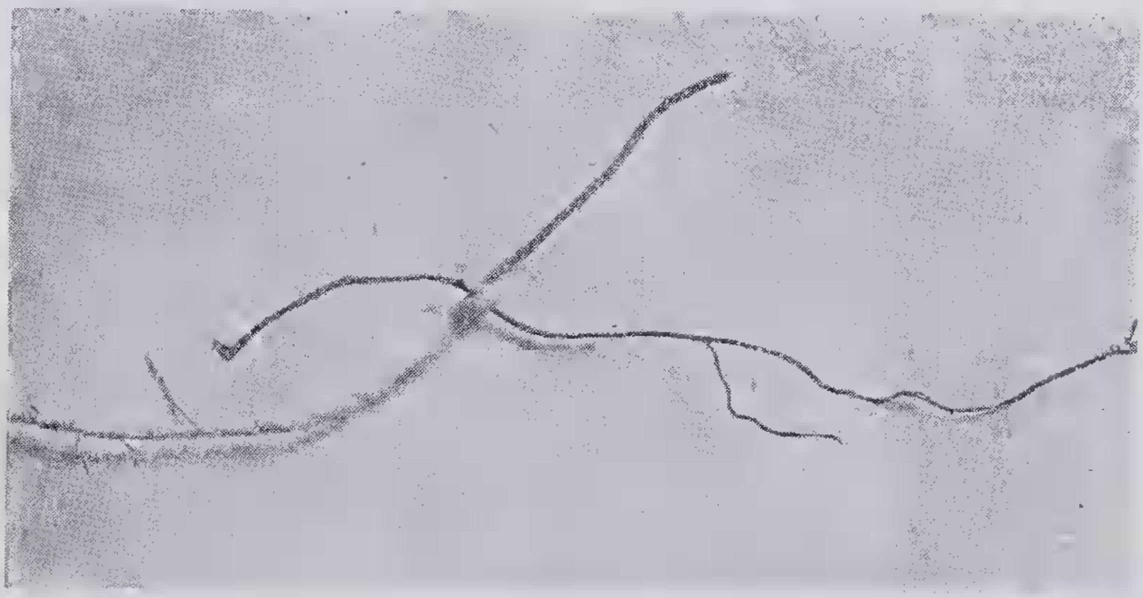
Figure 9.—Haustoriogen on a larger root (Melaleuca viminea). Part of the root has broken off, giving the haustoriogen the appearance of being the end of the small root.

There is nothing in the appearance of the tree to suggest a parasitic mode of nutrition. The leaves seem quite capable of supplying the organic food material necessary, as they are not deficient in chlorophyll, while the roots appear quite capable of supplying the mineral constituents necessary.

Roots are given off from the long underground stems and when they are traced out they are found to branch repeatedly, finally giving rise to long white fleshy roots up to about a quarter of an inch in diameter, and from these branch smaller white and very fragile roots. It is probably on account of the extremely fragile nature of these roots that the parasitic nature of the Christmas Tree has not actually been discovered previously. When they come into contact with another root, a fleshy outgrowth starts to develop. Two white fleshy arms start to grow round the attacked root in opposite directions from the point of contact (Fig. 7).

Ultimately the two arms meet on the other side of the root and fuse so that an unbroken fleshy ring encircles the host (Figs. 8 and 9).

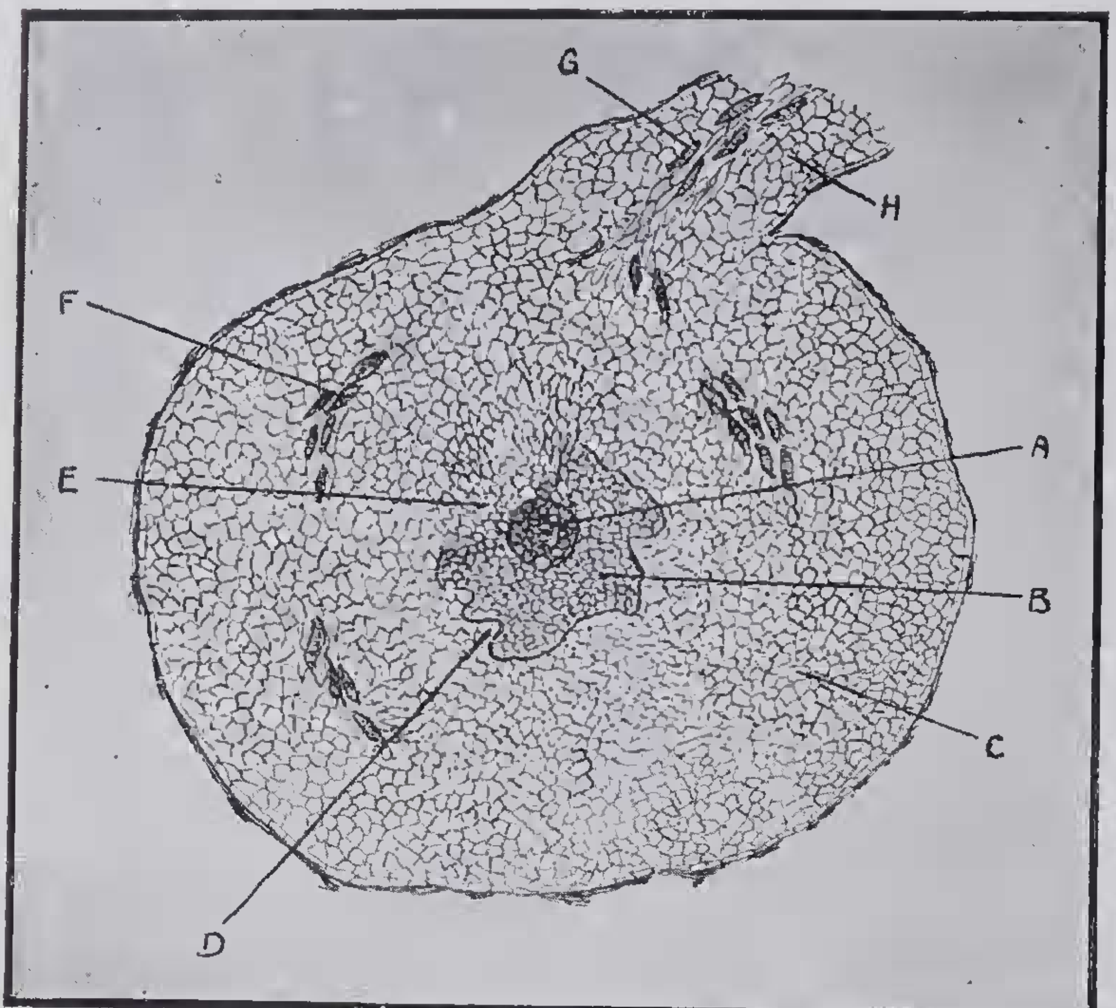
Fig. 8.



Haustoriogen on young root of Hibbertia hypericoides.

On the inner side of this fleshy ring, at the points of contact, arise the haustoria or suckers, so that it may for convenience be called the haustoriogen (Fig. 10). The haustoria are formed on the inner side of the fleshy arms before the ring is complete. The haustoriogen in section is found to contain a very small vascular bundle, which goes right round; but the greater part of it is composed of simple parenchymatous tissue. The haustoria are small tongue-like masses of parenchymatous tissue, and when they pierce the cortex of the host plant they appear to derive all food materials they obtain from it by simple osmosis. There is no fusion of the cells of host and parasite. The haustoria never go in as far as the wood. The wood is the channel of transference of water containing the organic constituents of plant life and the cortex and bast the means of transference of elaborated nitrogenous and non-nitrogenous organic food materials. The conclusion is that the main object of the parasitism of Nuytsia is to obtain an additional supply of organic materials, including nitrogenous substances.

Fig. 10.



Transverse section of haustoriogen attacking a root of Hibbertia hypericoides.

a, wood of host; b, cortex of host root; c, cortex of haustoriogen; d, haustorium in early stages of attack; e, haustorium in complete contact with cortical cells of host root; f, indications of vascular bundle of the haustoriogen; g, part of vascular bundle entering haustoriogen; h, cortex of root from which the haustoriogen has arisen.

In contrast to this is Nuytsia's close relation, Loranthus the Mistletoe. Here we have a plant parasitic for water and salts and quite well able to provide all the organic food materials it needs.

In this case there is vascular connection between host and parasite. It has been said that the Mistletoe may be more symbiotic than parasitic when it is on deciduous trees because it is evergreen and assimilates carbon dioxide in the winter when the host tree is leafless. The greatly decreased fruit crop in attacked apple trees proves that any symbiosis is greatly outweighed by the parasitism of the mistletoe. A more complete state of parasitism is shown by Cassytha, the Bush Dodder, which is common throughout Australia. This is a twining plant with green leafless stems. From the point of contact of its stem with the host arise haustoria. Here again there is vascular connection between host and parasite, the woods and phloems of each uniting. Cassytha is parasitic for both organic food materials and transpiration water containing inorganic salts. Both the Mistletoe and Bush Dodder are aerial parasites. The natural order Rhinanthaceae is notorious for the number of root parasites amongst its members. These, like Nuytsia, appear to have quite enough leaves to supply all the organic material necessary, but nevertheless need root connection to enable them to reach maturity. Their root system connects with that of the host root by means of disc-shaped haustoria. The fleshy ring giving rise to haustoria, as found in the Christmas Tree, is unique. The seeds of Orobanche, the Broomrape, another exotic root parasite, will only germinate when in contact with the roots of a host plant. This is certainly not the case with Nuytsia, the seeds of which will germinate out of contact with any host root.

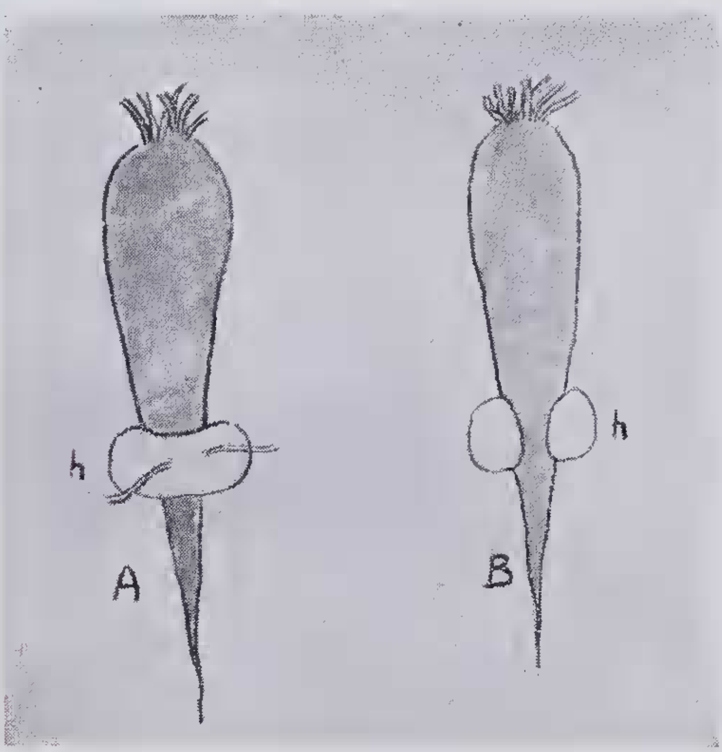
Seedlings are very rare and generally die off young. The survivors owe their success to having obtained connection with a host root early, while early death is often due to the failure of the root to find a host and the failure of the leaves to provide all the organic food materials necessary. One seedling at Mount Lawley was found to be drawing on the stem of the couch grass (Cynodon dactylon). This is interesting because it goes to show that the parasitic attacks of Nuytsia are not limited to roots. Seedlings may readily be distinguished from suckers by their stems, leaves, and rate of growth. The sucker appears above the ground as a stem about a quarter of an inch thick and grows rapidly so that in a year it is about four (4) feet high. Its pale leaves are few and sparsely scattered. A seedling, on the other hand, has a much thinner stem more closely beset with leaves, which are a brighter green than those of the sucker. One would expect the seedling to have more leaves and for these to contain more chlorophyll because it is more dependent on its own resources than is the sucker which has the reserve food material of the parent underground stem to draw on. The growth of the seedling is also much slower, a year-old seedling being several inches only in height and this is attributable to the same cause. Numerous attempts to raise seedlings of the Christmas Tree have been made but up to the present all have failed. The nature of the parasitism of the tree suggests a method of raising it successfully—the planting of the seed in a spot where its roots when formed will have easy access to the young roots of a plant which has been proved to be a host.

The haustoriogen is not the end of the Christmas Tree root. It is a lateral growth. The root continues to push its way through the soil to look for fresh victims. If it comes into contact with a large root it may run along the large host giving rise to a number of these parasitic outgrowths. Where the fleshy ring is developed round a root it grows in size but not in internal diameter, so that as the host root itself grows the haustoriogen acts as a ligature and gradually strangles it. It is a common thing to find a host root ending abruptly in the fleshy haustoriogen of the Christmas Tree, because the lower part, being strangled and starved, has died and rotted away. Sometimes a root attempts to ward off the attacks of the Nuytsia root by the development of cork and in some cases is successful in preventing the entry of the haustoria. If, however, the root is a small one, the haustoriogen ring may be formed just the same even though the haustoria cannot gain entrance, and the root is strangled by the ligature in time.

In its choice of hosts Nuytsia is very cosmopolitan. It attacks herbs, shrubs, and trees impartially. Exotics and natives, annuals, biennials and perennials, monocotyledons and dicotyledons are treated alike. I have found it attacking geraniums, roses, carrots, broad beans, black nightshade, sorrel (Rumex acetosella), couch grass, the so-called tree lucerne (Cytisus prolifera var. alba), vines, oranges, Hibbertia hypericoides, Banksia attenuata, Banksia Menziesii, Stirlingia latifolia, Melaleuca huegelii, Melaleuca viminea, Conostephium pendulum, Jacksonia furcellata, Calythrix flavescens, and Acacia pulchella. Further search will probably reveal it on a great many more species. Sometimes in its searchings for a host the Christmas Tree root comes into contact with another Christmas Tree root and attacks it in the same way that it would an ordinary root, but this is rare. It is analagous with the self-attack frequently noticed in such climbing parasites as Cassytha, the Bush Dodder, which nearly always recoils on and parasitises itself at some point or other. Very often the attack of the Christmas Tree is so strenuous that the host plant is starved and killed, in which case the fragile root which has given rise to the haustoriogen shrivels away, leaving the fleshy haustoriogen attached to the dead host root with hardly any sign of ever having had any connection. It looks at first sight like a fungal body, but a section shows its true nature by revealing the vascular tissue and the haustoria.

The haustoriogens are formed along the whole length of the underground stems and this accounts for their long life in the soil when the aerial parts have been removed. They can obtain all the organic and inorganic food materials they need without assistance of aerial shoots. Sometimes this underground stem can be traced along by the line of dead, dying, and weakened plants. In other cases the attack seems to cause the host plants very little inconvenience. The number of the roots affected is, of course, the deciding factor as to whether the plant will suffer or not. Sometimes nearly every root is surrounded by the haustoriogens of Nuytsia. At Como this is the case with banksias, ti-trees (Melaleuca viminea), and numerous other plants, both shrubs and herbs, many of which have been killed.

Fig. 11.



Carrots attacked by the haustoriogen of Nuytsia.
A, appearance of attacked carrot.
B, vertical section of same showing ligature effect of haustoriogen. h, the haustoriogen.

The rapidity of growth of the haustoriogen was shown in the case of the attack on some carrots at Como. These when only half-grown started to die off and on digging down it was found that the roots were surrounded by well-developed haustoriogens over half an inch in diameter (Fig. 11). The rapidity of development of these coupled with the large number produced along the length of the underground stems shows that Nuytsia is able to obtain a large amount of food materials from annuals and other small plants when growing as the solitary tree in a pasture.

Dr. Diels* is inclined to regard Nuytsia as being distinct from the Loranthaceæ and rather belonging to the common family from which both the Loranthaceæ and Proteaceæ have sprung. He summarises his objections as follows:—

> It (Nuytsia) cannot truly be said to belong to the real Loranthaceæ because of its fruit, and its habits remind one more of the Grevilleoidæ.

The difference of fruit does not seem sufficient reason for separating it from the family to which it is assigned, greater differences of fruit being shown in other families and which are regarded as generic and not ordinal. The flower is six-partite (the typical Proteaceæ have four (4) perianth segments), and is that of a Loranthus; in fact Labillardiere called the tree Loranthus floribundus.

With regard to habit, this is typically Loranthaceous in many points. Parasitism is characteristic of the family, and the discovery of this adds another link between Nuytsia and the other members. The leaves are very similar in their form and fleshiness, and the twigs of the Christmas Tree are very similar to that of Loranthus celastroides in appearance.

The underground stem may be compared with a similar structure in the mistletoe. The best investigated species of mistletoe is Viscum album, a European plant. The seeds germinate on a host plant; a sucker penetrates into the cortical tissues and bast and then stops. Subsequent growth of the branch results in the embedding of this sucker in the later-formed wood so that it appears to have pierced the wood. Lateral roots are given off and run along the cortex in both directions. At intervals along this cortical root arise aerial shoots; from the other side more sinkers go in as far as the wood, and further growth results in their being imbedded in the host wood also. This cortical root is analagous with the long underground stem of Nuytsia and shows similarity in habit of the two plants, when allowance has been made for the fact that Nuytsia is a terrestrial root parasite and that the mistletoe is parasitic on branches only. The conclusion is, therefore, that the structure and habits of the Christmas Tree are in accordance with its systematic placing in the Loranthaceæ.

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* Pflanzenvelt von W.A., 1906.